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SYSTEMATICS OF *LIOPHIS REGINAE* AND *L. WILLIAMSI* (SERPENTES, COLUBRIDAE), WITH A DESCRIPTION OF A NEW SPECIES

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ABSTRACT

The currently recognized species *Liophis zweifeli* is reduced to a subspecies of *L. reginae* and *L. oligolepis* is shown to be a junior synonym of *L. reginae semilineata.* Geographic variation in *L. reginae* is discussed in relation to major physiographic zones and the relationship of *L. reginae* to *L. epinephelus* is briefly discussed. *Liophis williamsi* is redefined, but its relationship to *L. reginae* is unclear. *Liophis andinus,* sp. nov., is described from the Cochabamba area, Bolivia.

INTRODUCTION

The species discussed herein have cis-Andean South American distributions. *Liophis williamsi* and a new species described herein occur in widely separated, middle elevation Andean locations. Whereas *L. reginae* also occurs at middle elevations, it is a species primarily of lowlands, from Colombia to Argentina. *Liophis reginae* has the widest distribution of any South American *Liophis.*

Liophis reginae has seven names associated with it that are principally based on variant color patterns. The descriptions of *violaceus* (Lacepede, 1789), *graphicus* (Shaw, 1802), *semilineata* (Wagler, 1824), *reginae macrostoma* (Amaral, 1935), *reginae maculicauda* (Hoge, 1954), and *zweifeli* (Roze, 1959) are based on color morphs, whereas *reginae*

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(Linnaeus, 1758) and *oligolepis* (Boulenger, 1905) are based on both quantitative and color pattern characters. *Liophis williamsi* has a single color pattern morph that is repeated in one population of *L. epinephelus* from Peru. *Liophis andinus* exhibits color pattern variation similar to that of *L. reginae.*

Liophis reginae is closely related to *L. epinephelus.* The latter species is discussed elsewhere (Dixon, 1983), but for the purpose of comparison with *reginae,* the following points obtain: the two species are similar in most characters in some parts of their ranges (Fig. 1A, B, C, and Table 1), but they are primarily allopatric, *epinephelus* being, in general, trans-Andean and *reginae* cis-Andean. The two species are parapatric along the eastern slope of the Ecuadoran Andes, principally in the upper Rio Pastaza and the upper Rio Santiago basins at about 1800 m. Where they are parapatric, their color patterns are not identical. *Liophis reginae* has a posterior lateral black stripe that occurs as a narrow border between scale rows three and four, whereas in *L. epinephelus* the stripe covers most of the third, from one-third to all of the fourth, and occasionally part of the fifth scale row.

SYSTEMATIC ACCOUNT

Liophis reginae (Linnaeus)

Distribution.—*Liophis reginae* is restricted to cis-Andean South America, where it occurs in every country except Chile and Uruguay. Its distribution extends from southern Brazil and northern Argentina to Trinidad and Venezuela (Fig. 2).

Lectotype.—The original description of *Coluber reginae* by Linnaeus (1758) gave the number of ventrals as 137 and subcaudals as 70. According to Andersson (1899), the Drottingholmense Museum (Museum Regis Adolphi Friderici I) has a jar labeled *C. reginae* that contains two young specimens of *L. reginae* (ventrals 137, 141; subcaudals 76, 81, respectively) and one young specimen of *Liophis lineatus.* Andersson (1899) thought that the latter specimen had been put among the young *L. reginae* by mistake because at first glance they appear similar. Andersson suggested that these were the specimens upon which Linnaeus based his description and by inference, the specimen with 137 ventrals should be the lectotype. Based upon the number of ventrals and subcaudals given by Andersson, there are two possible geographical areas from which the specimens may have come: the central coast zone of Brazil or the Suriname/Guyana area. The latter region is more likely because many of Linnaeus' South American specimens came from Suriname through the various directors of the East India Company (Holm, 1957). I accept Andersson's (1899) lectotype designation, and suggest the restriction of the type-locality to "Suriname."

Table 1.—*Variation in* Liophis reginae *and* L. epinephelus *for ventrals, caudals, and tail/total length ratios. Am. = middle and western Amazon, exclusive of Perú; Para = eastern Amazon; Mt. = Mato Grosso; NE = northeastern states; RJ = Rio de Janeiro region; SP = São Paulo region; Par/Argen. = Paraguay/Argentina sample. N = number in sample; M = mean; SE = standard error.*

Taxa and geographic origin	Ventrals				Subcaudals				Tail/total length ratio (%) (Adults only)			
	N	Range	M	SE	N	Range	M	SE	N	Range	M	SE
L. reginae												
Suriname	27	131–145	137.9	0.7	21	63–78	72.9	0.8	12	27.1–30.5	28.3	0.3
Guyana	22	129–147	138.7	0.8	13	68–80	75.1	1.1	9	25.5–30.5	27.7	0.6
Trinidad	12	137–146	142.6	0.7	7	77–83	80.0	0.8	5	24.4–30.0	28.4	1.0
Venezuela	31	132–148	142.3	0.6	23	69–88	79.9	1.2	21	24.1–31.0	28.1	0.3
Colombia	8	137–147	144.3	1.2	5	65–76	68.2	2.0	4	23.3–27.4	24.9	0.9
Ecuador	79	133–150	141.1	0.4	48	56–77	68.7	0.5	47	2.17–28.8	26.2	0.2
Peru	227	137–161	145.5	0.2	174	55–78	65.2	0.3	103	20.2–28.3	24.3	0.2
Am. Brazil	26	138–155	146.5	1.1	16	60–80	65.1	1.4	5	21.2–29.7	25.3	1.5
Para, Brazil	34	138–155	145.9	0.6	25	62–76	68.3	0.9	17	23.2–26.8	25.0	0.3
Bolivia	45	138–155	146.9	0.6	34	57–79	70.4	0.9	19	20.6–28.0	25.0	0.4
Mt. Brazil	29	145–160	149.8	0.8	21	70–85	74.3	1.6	12	21.3–29.7	25.3	0.6
NE Brazil	16	143–153	148.0	0.9	11	67–81	74.3	1.5	0	— — —	—	—
RJ Brazil	11	136–150	143.4	1.5	11	63–81	68.5	2.1	7	23.2–28.7	26.2	0.7
SP. Brazil	19	150–158	152.8	0.5	13	75–89	82.2	1.4	8	27.3–30.7	28.1	0.4
Par/Argen	10	150–159	152.4	0.8	9	77–91	80.9	1.4	7	23.3–28.7	26.7	0.6
L. e. juvenalis	51	139–152	145.0	0.4	45	51–62	56.0	0.4	25	18.9–25.2	21.5	0.2
L. e. pseudocobella	50	135–158	146.6	0.6	46	45–57	51.2	0.4	14	17.1–20.9	19.2	0.3
L. e. epinephelus	103	128–152	138.4	0.4	100	49–72	61.4	0.4	74	19.0–26.0	23.1	0.2
L. e. albiventris	93	141–165	150.7	0.5	83	52–70	60.3	0.5	63	19.1–24.2	22.0	0.2
L. e. fraseri	43	143–164	153.8	1.3	43	51–75	66.6	0.8	17	18.5–26.6	23.7	0.6
L. e. lamonae	48	141–157	149.7	0.7	41	51–67	59.2	0.7	22	20.2–24.1	22.2	0.2
L. e. opisthotaenia	32	142–152	147.0	0.5	29	53–78	64.7	0.9	17	20.2–25.6	23.6	0.3
L. e. bimaculatus	41	162–191	174.9	1.0	34	44–80	63.2	1.0	17	18.9–24.0	21.3	0.3

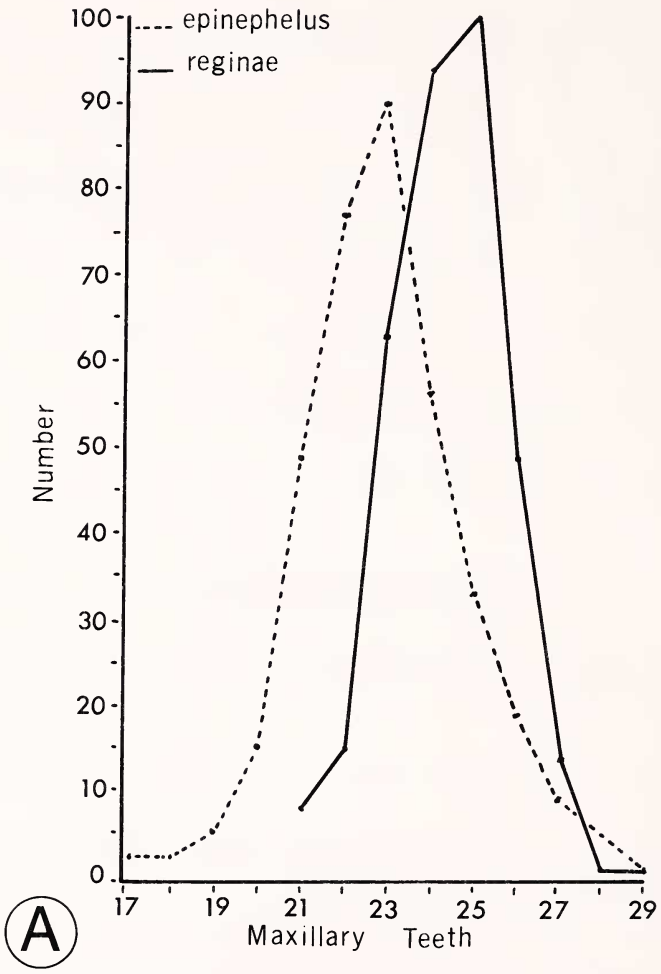
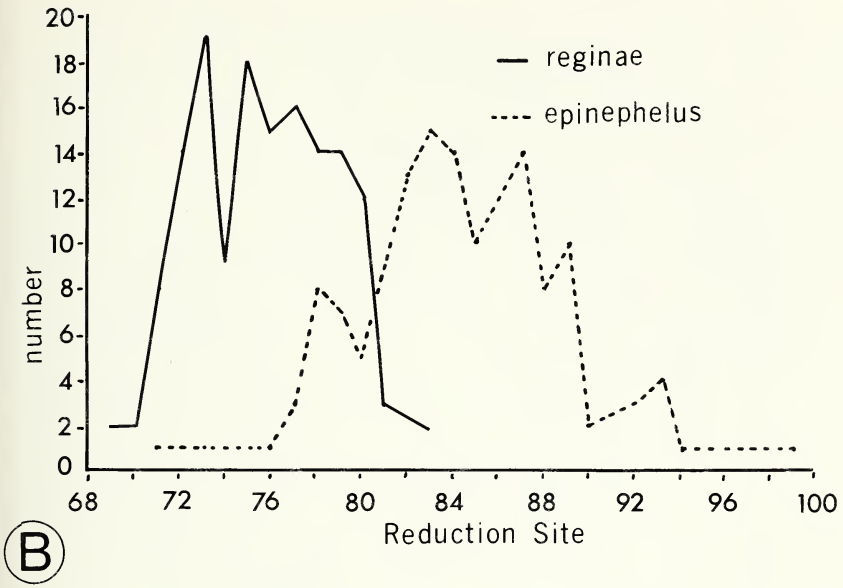


Fig. 1.—Comparison of *Liophis reginae* and *L. epinephalus* in: A) numbers of maxillary teeth.

Variation in color pattern.—The color pattern of 80% of the specimens examined of *L. reginae* consists of an olive to grayish green dorsum, with faint to well-marked dorsolateral diagonal black streaks or spots on the anterior one-third of the body. A thin black lateral line begins on the border of scale rows three and four on the posterior one-fourth of the body and continues to the tip of the tail. Occasionally, this line may be present only above the vent or slightly in front of it



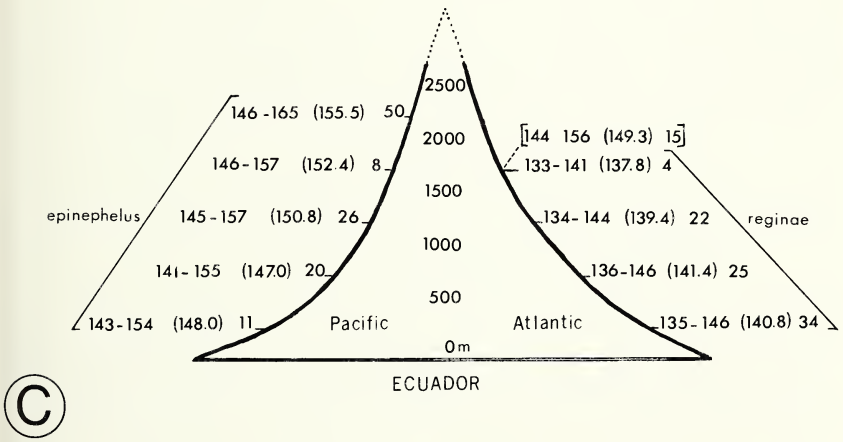


Fig. 1 (cont.)—Comparison of *Liophis reginae* and *L. epinephalus* in: B) comparison of the site of the reduction from 17 scale rows to 15; C) range and mean numbers (in parentheses, followed by sample size) of ventrals at various elevations along the Pacific and Atlantic versants of the Ecuadorean Andes (single set of numbers, in brackets on the right in 1C, represent the only population of *L. epinephelus* that appears to be parapatric with *L. reginae*).

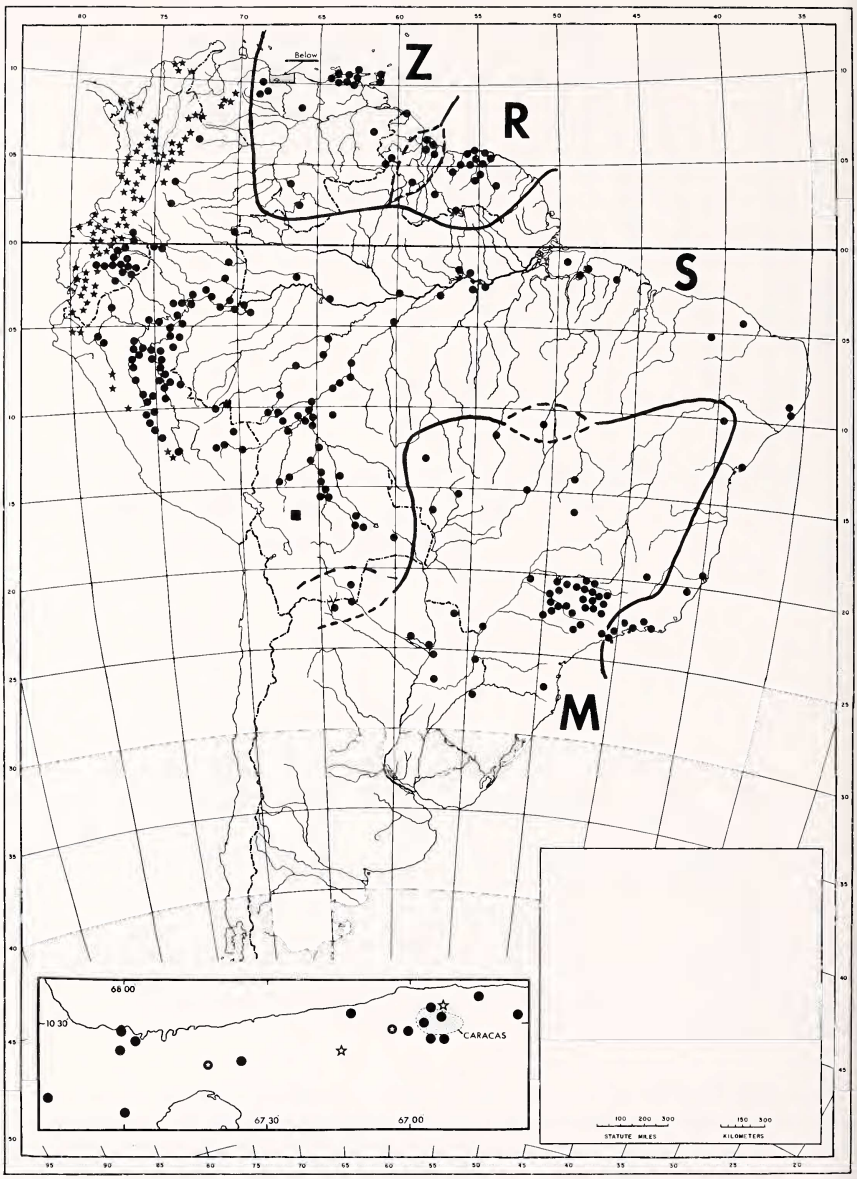


Fig. 2.—The distribution of *Liophis reginae, L. epinephelus, L. williamsi,* and *L. andinus* in South America. Circular dots represent the distribution of *L. reginae,* black stars represent *epinephelus,* and the square represents *L. andinus.* The insert shows the distribution of *L. williamsi* (open star) and sympatric localities of *williamsi* and *reginae*

thence continuing to the tip of the tail. The venter is checkered yellow and black in 95% of individuals and the subcaudal area is white. The ventral surface of some females in some populations is immaculate white (rare in males).

A sample of 100 individuals of *L. reginae* from Iquitos, Perú, contains at least three discrete patterns. One pattern is distinctly "salt and pepper" with each scale reddish anteriorly, greenish medially, and black posteriorly. Another pattern has the first and second scale rows pale green or yellowish green. The anterior part of the body is bright red and the posterior part dull green, with a black lateral stripe on the borders of the third and fourth scale rows continuing to the tip of the tail. The third pattern is the one previously described for about 80% of individuals. A combined form, with elements of all three patterns, can occasionally be found in a single individual.

The Peruvian sample seems to have the highest number (18%) of individuals with immaculate venters. Three hundred and two of 395 individuals have 17-17-15 scale rows and checkered venters. Sixty-nine males from Perú with 17-17-15 scale rows have checkered venters—none were immaculate white. The holotype of *L. oligolepis* Boulenger (Fig. 3D) is the only available male with the combination of 15-15-15 scale rows and a white venter. Of 107 Peruvian females with 17-17-15 scale rows, four have white venters and 103 are checkered; of 53 Peruvian females with 15-15-15 scale rows, 35 have white venters and 15 are checkered. These data suggest that scale row reductions and ventral color in Peruvian *reginae* is sex-linked in females, and only rarely so in males.

The subcaudal area is usually white, yellow, or salmon. However, specimens from the population in central Brazil and northwestern Argentina tend to have a few black spots on the outer edges of the subcaudals. In preservative, these spots appear as black smudges.

Geographic association of patterns seems to be discordant on the north and west sides of the Amazon Basin. The "salt and pepper" pattern is common in the coastal Andes of Venezuela (Fig. 3C), part of the Tepui region of the Guiana Shield, Trinidad, and extreme northern Guyana. However, this same pattern is present in the eastern middle slopes of the Andes of central Perú and continues southward into Bolivia. The pattern also shows up as an occasional variant in the mid-Amazon Basin, Iquitos area of Perú, and extreme western Venezuela.

(circle/white star) and localities of *reginae* (black circles). The heavy black lines denote the approximate boundaries of the subspecies of *L. reginae* (Z = *zweifeli*; R = *reginae*; S = *semilineata*; M = *macrostoma*). Dashed lines around circular dots represents zones of intergradation.

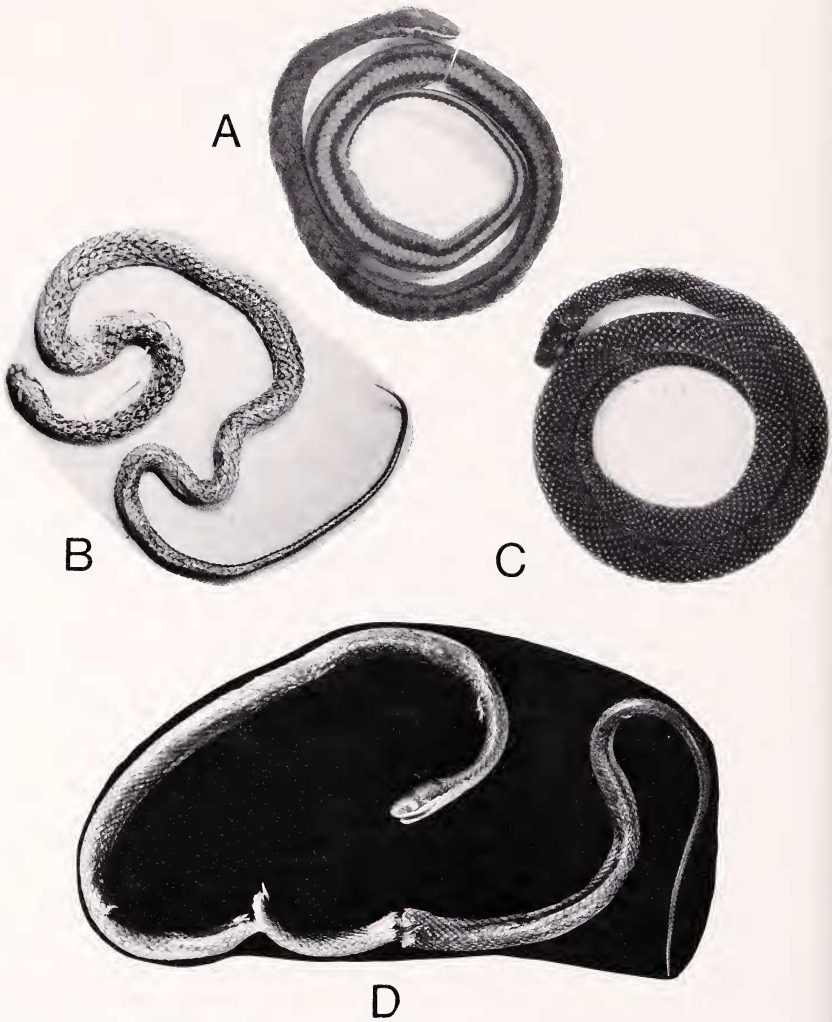


Fig. 3.—A) paratype of *Liophis williamsi* (MBUCV 3044), Rancho Grande, Venezuela. B) Holotype of *Liophis graphicus* (BMNH 1946.1.5.73), "America," represents *L. reginae reginae.* C) Holotype of *Liophis zweifeli* (MBUCV 95), Rancho Grande, Venezuela, represents *L. reginae zweifeli.* D) Holotype of *Liophis oligolepis* (BMNH 1946.1.4.66), Igape-Assu, Brazil, represents *L. reginae semilineata.*

The light-side, brightly colored pattern (Fig. 3B) is frequently seen in the lowlands of central and southeastern Perú, but more commonly in the Guianas (southern Guyana, Suriname, and French Guiana). The

latter pattern is supplemented with dorsolateral light flecking and/or dark spotting in Suriname and southern part of Guyana.

The typical pattern of an olive green dorsum with faint dorsolateral black streaks anteriorly and a thin, black lateral line posteriorly is prevalent throughout Amazonian South America in lowland situations, including the Amazon tributaries that extend into central portions of Brazil. The same pattern, but with a paler hue, is present in the Paraná drainage of Paraguay. Specimens from the Brazilian states of São Paulo and Paraná tend to have denser dorsolateral spotting anteriorly, brighter colors, and the subcaudals more often smudged with black.

A single female specimen of *L. reginae* from Tobago (USNM 228069) has an atypical color pattern. It resembles the pattern of *L. epinephelus lamonae* (*sensu stricto,* Dixon, 1983) from the middle elevations of eastern Colombia. The dorsal pattern (at 100th ventral) consists of the first and second scale rows olive green; third scale row olive green with a large black smudge in the middle of the scale; fourth scale row tan (cream in life?) with the lower edge black; fifth scale row tan with the upper one-third with greenish black flecks; sixth to tenth scale rows olive green. The ventrals and subcaudals are immaculate cream. The absence of black marks on the ventrals that are typical of most *L. reginae,* may be sex-linked as indicated for females with immaculate ventrals from the Amazon Basin (this paper). The dorsolateral tan stripe is the most striking difference between the patterns of the specimens from Tobago and *L. reginae* from Trinidad (the latter lack this stripe).

Other characters of the Tobago specimen follow: 27 maxillary teeth, 17-17-15 scale rows, 143 ventrals, 77 subcaudals, 8-8 subcaudals, 8-8 supralabials, 9-10 infralabials, 4+5 supralabials entering orbit, 1+2 temporals, 1-1 preoculars, 2-2 postoculars, divided anal plate, 482 mm in total length, 120 mm tail length; 0.270 tail/total length ratio. All of the latter characters are typical for most samples of mainland and Trinidadian *L. reginae* (see Tables 1 and 2). Hardy (1982) has commented on this specimen and presented a photograph.

Scutellation variation.—The number of head scales varies little between and among samples of *L. reginae* from throughout its geographic range. The distribution of the numbers of head scales (Table 2) of *L. reginae* is typical for most species of *Liophis.*

A comparison of the usually sexually dimorphic characters (ventrals and caudals) between males and females of *L. reginae* from Amazonian Perú (sample of 67 ♂♂ and 174 ♀♀) reveals no significant differences in mean numbers. Therefore, sexes were combined for analyses of these characters in sample by sample comparisons. An examination of the average number of ventrals throughout the cis-Andean distribution of *L. reginae* (Fig. 4) shows that the Amazonian population (samples 7–

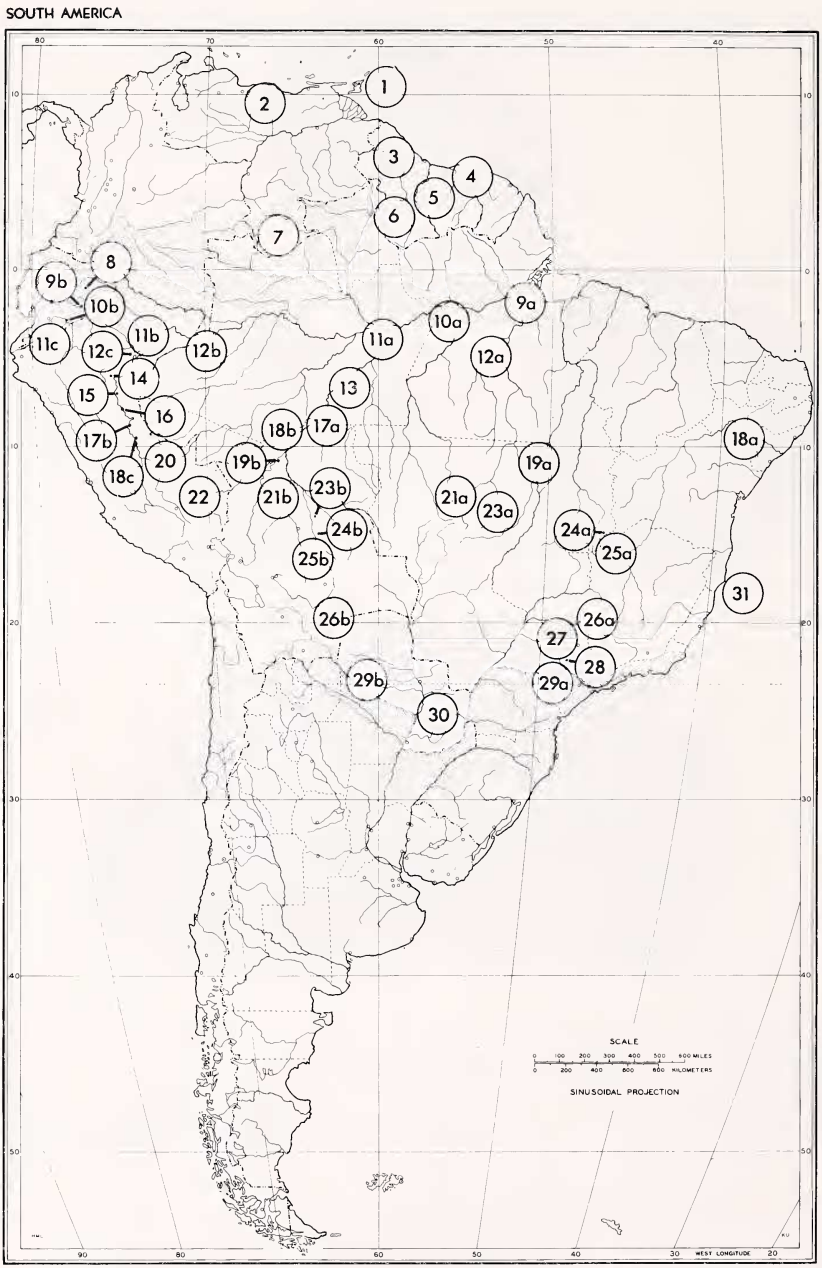


Fig. 4.—A) Geographic locations of samples of *L. reginae,* arranged by latitude from North to South, and by longitude from East to West.

Fig. 4.—B) Univariate analysis of ventrals and subcaudals arranged in order of the samples Fig. 4A. Horizontal line represents the range of variation, vertical line the mean, black rectangle two standard errors on either side of the mean, open rectangle one standard deviation on either side of the mean.

Table 2.—*Variation in numbers of head scales in* Liophis reginae. *Numbers in parentheses = sample size.*

Preoculars	1-1 (477)	1-2 (5)	2-2 (3)						
Postoculars	1-1 (2)	1-2 (1)	2-2 (482)	2-3 (1)					
Supralabials	6-7 (1)	7-7 (1)	7-8 (4)	7-9 (1)	8-8 (468)	8-9 (6)	9-9 (5)		
Infralabials	8-8 (5)	8-9 (5)	8-10 (2)	8-11 (1)	9-9 (12)	9-10 (32)	10-10 (426)	10-11 (5)	11-11 (3)
Supralabials Enter orbit	$\frac{3+4+5}{4+5}$ (2)	$\frac{3+4}{4+5}$ (4)	4+5 (465)	4+5+6 (3)	$\frac{4+5+6}{5+6}$ (1)	$\frac{4+5}{5+6}$ (7)	$\frac{4+5}{4+5+6}$ (2)		
Temporals	1+1 (5)	$\frac{1+1}{1+2}$ (18)	1+2 (462)	2+2 (1)					

19) is intermediate, with ventral numbers increasing to the south and decreasing to the northeast (samples 3–6). The greatest difference between adjacent samples is between Suriname and eastern Amazonia. I have not examined, however, specimens from the area between Belém, Brazil (sample 9a), and French Guiana (sample 4). There may be a cline in ventral number between these two regions, or perhaps partial gene flow around the Guiana Shield. There do not appear to be well-defined steps in the ventral counts of the cis-Andean populations, except the Venezuelan-Trinidad versus the Guyana-Surinam samples, and the coastal Brazil sample (sample 31), and its adjacent, but allpatric samples (samples 24a, 26a, 27, 28, 29a) from inland southeast Brazil. The latter discordance is observed in several other species of snakes with similar distributions (*Typhlops brongersmianus, Chironius fuscus, Liophis miliaris, Liophis poecilogyrus*). Geological and other historical evidence suggests that the vegetation and climate of that particular coastal zone of Brazil was probably connected to the Amazonian Forest within the past few thousand years, and gene flow between populations of both areas was relatively recent or perhaps continuous to the present time (Dixon, 1979).

The number of subcaudals also shows both concordant and discordant variation patterns (Fig. 4). *Liophis reginae* samples from northern Venezuela, Trinidad, and eastern Venezuela (samples 1, 2, 7) have high numbers of subcaudals. Adjacent Guyana, Suriname, and Colombia snakes (samples 3, 4, 5, 6, 12b) have low numbers of subcaudals, as do those from the Atlantic coastal zone of Brazil and most of western cis-Andean South America. Paraguay and eastern Brazil (exclusive of Atlantic Coast) samples have high numbers of subcaudals. Samples of *L. reginae* from south of the Amazon Basin suggest that there is little gene flow as expressed in subcaudal numbers, between the caatinga/cerrado populations of Brazil and the southern Perú/eastern Bolivia populations along any given latitude between 10° to 20°S. Samples from near Isla Bananal, Brazil (19a) and northern Argentina (29b) tend to be intermediate between western South American samples (18b, 18c, 19b, 20, 21b, 22, 23b, 24b, 26b) and eastern South American samples (18a, 21a, 23a, 24a, 25a, 26a, 27, 28, 29a, 30). The difference observed may be an artifact of combined samples along the various latitudes or they may reflect true differences between allopatric samples. In either case, the result appears as a "rassenkreis" (Fig. 4) because adequate samples are not available from Pantanal region of western Brazil, eastern Bolivia, and northern Paraguay. The tail length/total length ratios follow the same pattern as the subcaudals, but the numbers of maxillary teeth are totally discordant.

Two hundred twenty seven *L. reginae* from the Peruvian Amazon show a relatively smooth, north to south, cline in most characters

examined. The number of ventrals, subcaudals, and tail length/total length ratios increase (11b, 12c, 14, 15, 16, 17b, 18c, 22), whereas the number of maxillary teeth decreases. A comparison of large samples (Ecuador versus Perú) suggests that some characters of the populations between these two countries are significantly different. However, when subsets of the adjacent samples (northern Perú, southern Ecuador) are compared, there is a relatively smooth cline between the samples. This merely suggests that some of the significant differences between samples are the result of clustering of subsets of samples by country, and not by geographic zones. The entire Amazon sample shows little variation from east to west along the same latitude and vegetation zone (9a, 10a, 11a, 11b, 12a, 12b, 12c). However, considerable north to south variation is noted along different latitudes.

Allocation of names.—There are seven names associated with *L. reginae* (the names listed below are those recognized as subspecies, and synonyms):

reginae reginae (Linnaeus, 1758; Fig. 3B)
violaceus (Lacepede, 1789)
graphicus (Shaw, 1802)

Guyana, Suriname, and French Guiana

reginae semilineata (Wagler, 1824; Fig. 3D)
oligolepis (Boulenger, 1905)

Amazonian Ecuador, Colombia, Perú, Bolivia, Venezuela, Brazil, also Atlantic Forest of Brazil

reginae macrostoma (Amaral, 1935)
reginae maculicauda (Hoge, 1954)

Chaco Boreal and Cerrado vegetation of Brazil, Argentina, Paraguay, and Bolivia

reginae zweifeli (Roze, 1959; Fig. 3C)

Montane zones of Venezuela and Trinidad

Three names, *ornata* (Jan, 1863), *viridicyanea* (Jan and Sordelli, 1866), and *maculata* (Steindachner, 1867), assumed to be varieties of *L. reginae,* belong to other species. The holotype of *ornata* (MHNG 108:39) was examined and found to be an example of *L. miliaris.* The holotype of *viridicynaea* has not been located, but the color pattern, squamation and illustration furnished by Jan and Sordelli (1866) indicate that this name belongs to *L. poecilogyrus.* The syntypic material of *maculata* is apparently lost. Franz Tiedemann of the Austrian Natural History Museum (personal communication) stated that they have

no Natterer material from "Ypenema," Brazil, the type locality, but have 32 specimens of *L. reginae* collected by Natterer from other Brazilian localities. A detailed examination of Steindachner's (1867) description of *maculata* suggests that he had more than one species present, and possibly two genera. He speaks of scale rows around the body and subcaudal number as 15 and 62–68 in young individuals and 17 and 80–90 in old specimens, respectively, and of highly variable color patterns. The squamation and color descriptions presented could represent Brazilian *Rhadinaea* as well as *Liophis*. Until Steindachner's series of specimens are located, his name must reside as *species inquirendae*.

Key to subspecies.—The following key is provided to aid in recognizing subspecies of *L. reginae*. The characters utilized are those that are average for those populations occupying specific geographic areas (Fig. 2).

1. Dorsum spotted with black and yellow; black lateral caudal stripe faint or absent 2
– Dorsum greenish, olive, grayish, never yellow and black spotted; black lateral caudal stripe always present and distinct 3
2. Subcaudals average 80 (69–88), (Venezuela, Trinidad, northern Guyana) . . *zweifeli*
– Subcaudals average 65 (55–78), (cis-Andean middle slopes of Perú and Bolivia) . . . . . *semilineata*
3. Scale rows one and two pale colored 4
– Scale rows one and two colored like rest of dorsum 5
4. Dorsum with dense pale and dark paravertebral flecking, subcaudals average 74 (63–80), (French Guiana, Suriname, Guyana) . . . . . *reginae*
– Dorsum without dense pale and dark paravertebral flecking, subcaudals average 67 (57–71), (Amazonian lowlands of central and southern Perú) . . . . . *semilineata*
5. Subcaudal area with ventrolateral black spots, flecks, or smudges, subcaudals average 81 (75–91), (southern Goiás, São Paulo and south and southwest Paraná, Brazil and Argentina) . . . . . *macrostoma*
– Subcaudal area immaculate, subcaudals average 70 (55–81), (Amazonian South America and Atlantic coastal Brazil) . . . . . *semilineata*

Liophis williamsi (Roze)
Fig. 3A

Distribution.—*Liophis williamsi* is known only from the ground-floor leaf litter of cloud forest zones of the eastern Andes of Venezuela, from Rancho Grande, Aragua, to Cerro El Avila, Distrito Federal (Fig. 2).

Type series.—Roze's (1958) name is the only one that has been applied to this species. Marcuzzi (1950) mistakenly discussed this species under *Leimadophis bimaculatus opisthotaenia* (=*L. epinephelus*), a species that occurs in the western part of the Venezuelan Andes near Mérida.

I have examined the type series and four additional specimens. There is strong sexual dimorphism in the number of ventrals and subcaudals,

but not in tail length/total length ratios, maxillary teeth, or color pattern.

Variation.—The ventrals of four males vary from 155–169 (mean = 160.3); subcaudals vary from 58–66 (mean = 60.8). Three females have ventrals that vary from 146–150 (mean = 147.4); subcaudals 53–62 (mean = 58.0). The maxillary teeth vary from 19–22 (mean = 20.5). The tail length/total length ratios (%) vary from 20.7–22.6 (mean = 21.7). There are no scale row reductions, all specimens having 17-17-17 dorsal scale rows. Supralabials, supralabials entering orbit, loreals, and postoculars are invariably 7, 3+4, 1, 2, respectively. The anal plate is divided. The infralabials vary as follows: 9-9 (4), 10-10 (2); preoculars 0-1 (1), 1-1 (4), 2-2 (2); temporals 1+2 (6), 1+1 (1). Maximum total length is 465 mm in males and females.

Pattern.—The dorsal color pattern consists of anterior blackish spots, bars and/or blotches surrounded by a dark brown ground color. At midbody the darker spots tend to form black paravertebral lines on scale rows seven or seven and eight. The zone between the fourth and seventh scale rows is pale brown or yellowish brown, the upper half of the fourth scale row is pale yellow, lower half of fourth and upper two-thirds of third black, lower one-third of third yellowish, and all of second and first scale rows brown. The dorsolateral dark stripes unite above the tail and form a single line to the tip of the tail. The dorsal surface of the head varies from brown to blackish brown, with or without obscure black spotting. A black line extends from below the nostril to the last supralabial and occasionally onto the nape, usually covering the upper one-fourth of the supralabials. The middle portion of the supralabials is white, whereas the lower one-third may be entirely black, or white with large black spots concentrated on the central portion of the lower one-third of each labial. The white area of the supralabial may extend past the last supralabial to the third or fourth scale row of the nape. The infralabials may be entirely black, or mostly black with white edging. The chin and throat may be white with a few black marks, or almost entirely black with a few white-edged scales. The venter and subcaudal surface may be completely white with a few black flecks, or venter densely spotted with black on a gray to pinkish ground color with the subcaudals gray, with or without a midventral black line extending from anal plate to tip of the tail.

Hemipenis.—The hemipenis has a smooth apical disc, and a sinistral sulcus that forks one-third to one-half its distance from the base. The structure is very spinose, without calyces. Roze (1958) indicated that the specimen he examined had a calyculate zone near the apex of the *sulcus spermaticus,* but neither Myers (1974:20) nor I have been able to locate such a zone on the specimens we have examined.

Comments.—A color pattern similar to that of the head and trunk of *L. williamsi* is also present in *L. epinephelus fraseri* from central Perú. The patterns are so similar that I originally thought *L. williamsi* was represented by two widely disjunct allopatric populations. However, after examining a large number of individuals of the *L. reginae* group, I am convinced that pattern types within this complex are repetitive within and between species, and pattern alone will not insure proper identification.

One additional species seems related to this complex, an altitudinal isolate from Cochabamba, Bolivia, that shows a scale row reduction mode similar to that found in some individuals of *L. reginae.* The general shape of the head and body, the tail/total length ratios, and variable color pattern suggest a relationship to both *L. reginae* and *L. epinephelus.* I designate this undescribed population as:

Liophis andinus new species
Fig. 5 and 6

Holotype.—Carnegie Museum of Natural History (CM) R2808, adult male, from Incachaca, 2500 m, Cochabamba, Bolivia, collected by J. Steinbach in October 1921.

Paratopotypes.—CM R2777, R2797–98, R2780–81, R2804–07; American Museum of Natural History 36012, 36014, 36016.

Distribution.—Known only from the type-locality (Fig. 2).

Diagnosis.—*Liophis andinus* is distinguished from all species of *Liophis* except *L. reginae* by having 15-15-15 dorsal scale rows, generally without reduction (one reduced to 14 posteriorly), rather than 19-17-17, 19-17-15, 17-17-17, or 17-17-15 dorsal scale rows; and from all species of *Liophis* by having three (very rarely two) supralabials entering the orbit rather than two.

Description of holotype.—Adult male, total length 485 mm; tail length 130 mm; tail/total length ratio 0.268; head length 15.8 mm, head width 8.0 mm; diameter of orbit 2.7 mm; nostril to eye distance 2.8 mm; ventrals 150, subcaudals 68; supralabials and infralabials 8-8; preoculars and postoculars 2-2; temporals 1+2; loreal 1-1; third, fourth, and fifth supralabial entering orbit on each side; maxillary teeth 24, last two enlarged and separated from remainder by a diastema equal in width to the basal length of three prediastemal teeth; *in situ* hemipenis 9 subcaudals in length, slightly bilobed, forked *sulcus spermaticus,* naked basal pocket, smooth distal, apical disc. Color pattern (in preservative) as follows: top of head brown or olive brown, side of head with broad black streak from edge of rostral, through eye to above and/or slightly beyond last supralabial; upper edge of preocular with small cream spot; infralabials, throat and first few ventrals immaculate cream;

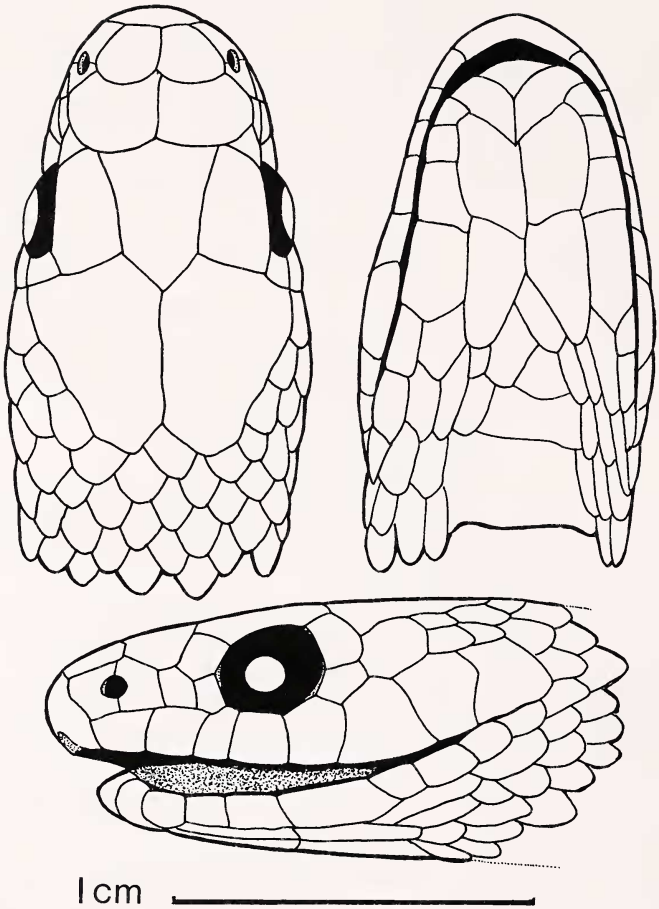


Fig. 5.—A dorsal, ventral, and lateral view of the head of the holotype of *Liophis andinus* (CM R2808).

supralabials cream except for dorsal edge which is black; midbody pattern consists of cream ventrals with dark scattered flecks; upper edge of first scale row and lower edge of second scale row with small black dot at their alternate apexes, a thin black edge on each of these two scale rows connects the small black dots, giving an appearance of a zigzag line; upper half of third and lower third of fourth scale rows with straight-edged black line; upper third of sixth and all of seventh scale rows black, lower edge straight, upper edge undulating; eighth (middorsal) scale row faintly speckled, otherwise cream; lateral interspaces

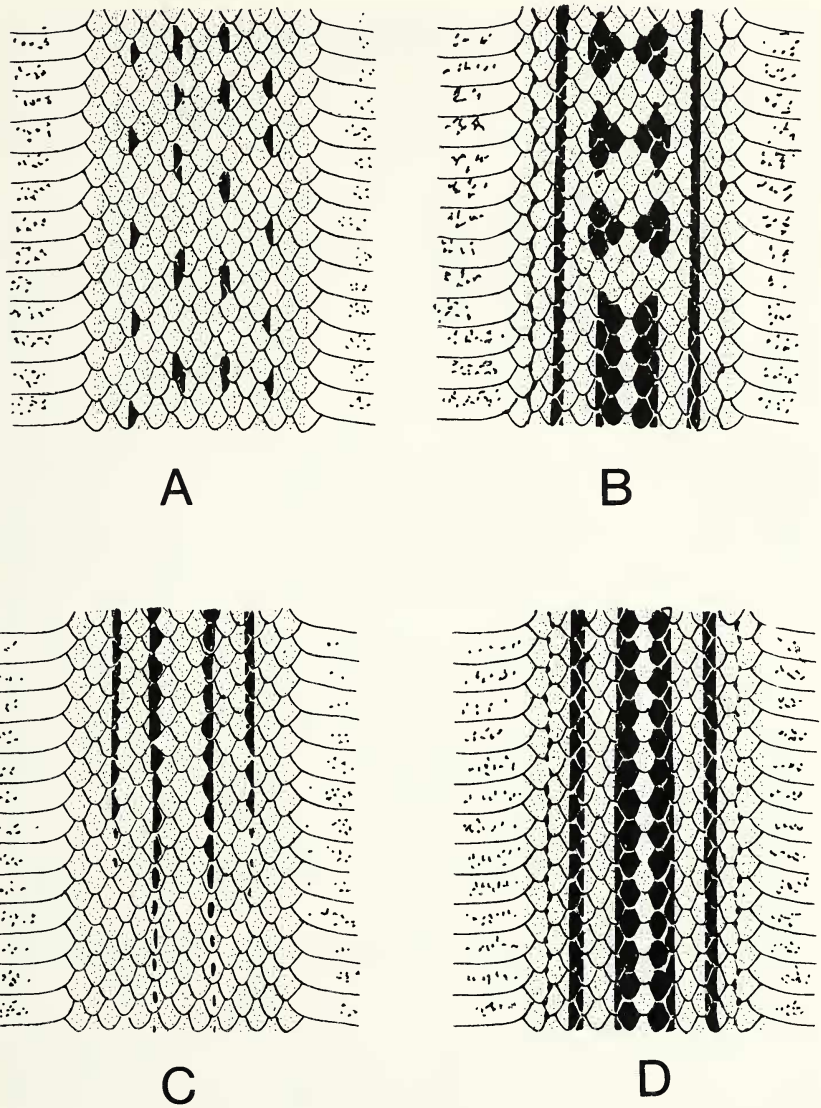


Fig. 6.—The midbody color patterns of the type series of *Liophis andinus* with the exception of CM R2797 which appears to be patternless. A) represents CM R2798; B) CM R2780; C) CM R2781, R2804, R2806–07, AMNH 36012, 36014, 36016; D) CM R2777, R2805, R2808.

between black lines probably cream, but specimen is darkened in formalin and light ground colors are obscure; black stripe of third and fourth scale rows continues onto the tail where it occupies the upper half of the first and lower tip of the proximal lateral caudal scales, and passes through the middle third of the first scale row distally; subcaudals immaculate cream.

Variation.—The following data are based upon the type series; means and sample size are in parentheses, measurements in millimeters; total length of five males with complete tails 406–570 (490.0), seven females 445–700 (606.6); tail/total length ratios of males 0.268–0.283 (0.272), females 0.238–0.261 (0.253); head length of both sexes 14.4–21.6 (17.8); head width 8.0–11.7 (10.0); nostril to eye distance 2.8–4.9 (4.3); diameter of orbit 2.7–4.9 (4.28); head width/head length ratios 0.51–0.59 (0.543); ventrals of males 148–151 (149.8), females 153–156 (154.6); subcaudals of males 67–72 (70.1), females 64–68 (65.8); maxillary teeth of males 23–26 (24.3) females, 24–27 (25.0). Scale features of the head vary as follows: preoculars 1-1 (8), 1-2 (1), 2-2 (4); postoculars 2-2 in all; loreal 1-1 in all; supralabials 8-8 (11), 7-8 (1), 8-9 (1); infralabials, 8-8 (8), 7-7 (1), 7-8 (1), 8-9 (1), 9-9 (2); temporals, 1+2 (11), 1+3 (2); supralabials entering orbit, 3+4+5 (11), 3+4+5/4+5+6 (1), 3+4/3+4+5 (1).

The color pattern is obscure in most specimens because of darkening by formalin. However, "in fluid" observation of the pattern reveals at least five midbody patterns (Fig. 6, unicolored pattern not figured), of which figures C and D represent about 83% of the individuals. The venter appears to be cream or yellow with some dark flecking in all individuals. The subcaudal area appears to be immaculate cream or yellow. The cream or yellow spot on the upper edge of the preocular is distinct in 10 individuals and obscure in three. In one specimen, an obscure cream spot also appears on the upper edge of the suprapostocular.

The *in situ* hemipenis varies in length from 8 to 9½ (8.5) subcaudals. It is slightly bilobed, the lobes usually indicated at the level of the seventh or eighth subcaudal. The *sulcus spermaticus* divides about the level of the third subcaudal. There is a naked basal pocket present in all specimens. There seem to be six proximal rows of relatively large spines while the remainder of the hemipenis is covered with densely set, smaller spinules. The outer edge of the distal end of the hemipenis bears a relatively large, smooth apical disc.

Specimens Examined

Liophis andinus.—Bolivia: Incachaca, AMNH 36012, 36014, 36016, CM R2777, R2797–98, R2780–81, R2804–08.

Liophis reginae macrostoma.—ARGENTINA: "northern," MHNG 1552.34; Iguazu Falls, FMNH 9252, 9379; Puerto Iguazú, IML 194. BRAZIL: no specific locality, MCZ 1991; Agudos, KU 124638; Anhangaí, MZUSP 1659; Annapolis, AMNH 62230, 62233; Aruaña, MZUSP 2182; Assis, USNM 165586; "Bahia" BMNH 149.80, MCZ 2952; Burití, MZUSP 5352; Corumbataí, MZUSP 4007; Crato, MZUSP 5244; Franca, MZUSP 828; Itaqua, USNM 100752; Pirapora, MZUSP 829; Posto Diauarum, MZUSP 3691–92, 5512, São Felipe, MZUSP 5715; São Luis de Cáceres, MZUSP 1370; "São Paulo", MCZ 17809–10, UMMZ 62817–18; Taubaté, USNM 76390; Usina Sinimbú, Mangabeira, MZUSP 2940–42, 3337; Utiarití, MZUSP 4743; Vespasiano, MZUSP 2776; Xavantina, BMNH 1972. 4.20. PARAGUAY: Asunción, BMNH 1930.11.27.202, FMNH 13160; Primavera, BMNH 1956.1.3.34, 1960.1.3.39, 1962.80; Rosario, BMNH 1962.82; 2.7 km N San Antonio, UMMZ 14321.

Liophis reginae reginae.—FRENCH GUIANA: Maripasoula, MCZ 77512. GUYANA: no specific locality, AMNH 3595, 17680; Acarahy Mountains, KU 69825; New River BMNH 1939.1.1.87–88, Wismar, UMMZ 77506 (2). SURINAME: no specific localtiy, MCZ 16387, RMNH 12510, USNM 5434, 6117; 3 km SE Blakawatra, RMNH 1877; Brokabaka, RMNH 1859; Brokopondo, MCZ 149538, 152599–601; SE of Carl Francois, RMNH 1841; Lely Mountains airstrip, RMNH 1650; 12 km NE Lely Mountains airstrip, RMNH 1682; Lelydrop, AMNH 104623; Loksihatti, RMNH 771; 13 km W Moengo, RMNH 387; Republiek, Para Kreek, RMNH 84; R-V Nature Reserve, Foenjue Island, Coppename River, MCZ 152601; Sam Kreek, AMNH 104621; Uitkyk, CM 44301; Zanderij, BMNH 1946.4.4.54.

Liophis reginae semilineata.—BOLIVIA: no specific locality, AMNH 2985, 4440; Abuná, UMMZ 56874; Buena Vista, UMMZ 60721–22, 64153 (2), 67910–16; AMNH 36006, FMNH 35690, 35702; "Beni, AMNH 101877; Cachuela, AMNH 22523; Cauriaco, AMNH 101875; Chamblaya, BMNH 1902.5.29.96; Chiquitas, FMNH 195908; Coretolla, AMNH 101837; Guayara Merin, USMN 123970; Huachi, AMNH 22473, 22479, 22503; La Perseveranda, AMNH 101833; Las Yungas, CM 19, 24, 27; Manao, UMMZ 56870–72, 56882; Riberalta, AMNH 22257; Río Iténez, AMNH 101873; Río Madre de Dios, UMMZ 56886, 59786; Río Mamore, AMNH 101835; Rurrinabaque, AMNH 22445, 22522, Sacramento, MZUSP 4151; 10 km E San Antonio, AMNH 101874; 10 km W San Pedro, AMNH 101834; 4 km N Santa Cruz, AMNH 101836; Santa Rosa, AMNH 101830–32, 101838–40; Trinidad, AMNH 101876. BRAZIL: no specific locality, MNHP 1912-483, 1912-484, 1912-485, 1912-485A, 1912-485B; Abuná, UMMZ 56877; "Amazonas", AMNH 14543; north bank of Amazon, three hours downstream from Leticia, Colombia, LACM 103621; Angra dos Reis,

MZUSP 2419; "Bahia," BMNH 62.1.30.57. MCZ 3285, Bahia, AMNH 22281; Barcarena, KU 128102; Barra do Tapirapés, AMNH 93575–83, MZUSP 3799, 4326, 4336; Belém, KU 127273–74, 124593, 124599, 128103, 140180; 50 km from Belém, MCZ 53200; Boca do Acre, MZUSP 5754; Cachimbo, MZUSP 3335–36; Calama, MZUSP 5901; Campo Novo, MZUSP 5924; Canindé, MZUSP 4238–40, 4251, 4276, 4282; Canutama, MZUSP 5762; Foz do Jamarí, MZUSP 5905; Hyutanahã, USNM 28945; Igapo-Assú, BMNH 1946.1.4.66; Igarapé Belém, AMNH 115019–21; Lago Catu, MZUSP 1826; Manaus, AMNH 64897, CAS 49796; MZUSP 3053; Marajo Island, BMNH 1923.11.9.117–21; Mavés, AMNH 89784, 91643–44; Novo Aripuanã, MZUSP 5917; Óbidos, MCZ 1204 (2), 2574 (2), UMMZ 56310; Oriximiná MZUSP 5487; Pacotí, MZUSP 3632; "Pará," BMNH 45.8.25, MCZ 898, 1171, 2880, 2882, 3292, 5690; Plácido de Castro, MZUSP 2556; Porto Velho, MZUSP 3751–52, 4632; Porto Velho, MZUSP 3691–92; Puruzinho, MZUSP 5908; Río Branco, MZUSP 2555; "Río de Janeiro," MCZ 3944, 6792; Río Doce, MCZ 17957, MZUSP 830; Río Jurúa, MZUSP 833; San Carlos, MZUSP 5904; Santa Leopoldina, MZUSP 832; Santarém, MCZ 1162 (3), 3682, MZUSP 1250; Tapaúa, MZUSP 5769; Valença, MZUSP 5812–13. COLOMBIA: "La Selva," MCZ 62256; Leticia, AMNH 78986, 95075, KU 124938, LACM 103622, MCZ 48978–80, 57249; Tarapaca, CAS 135343. ECUADOR: no specific locality (or doubtful locality), AMNH 15210, 24147, BMNH 89.4.8.1. (2), LACM 2540; Abitagua, FMNH 25812–14, 28025, 28060; Alpayacu, FMNH 4069; Arajuno, USNM (JAP) 776; Baños, UMMZ 88964; near Baños, UMMZ 92021, 92023; between Baños and Abitagua, UMMZ 92024–27, 92030; Cabeceras del Río Arajuno, USNM (GOV) 8304–05, 8310; Cabeceras del Río Capahuari, USNM (GOV) 7225, 7413; Canelos, USNM (GOV) 7327; Chichirota, USNM(GOV) 7296, 7416; Concepción, USNM (GOV) 7325; Copataza, USNM (GOV) 7280–82; Dureno, KU 105413; El Topo, BMNH 1912.11.1.36–39; Lago Agrio, KU 126035; Limóncocha, UIMNH 54665, 61248–51, 61253–56, 63524, 82477–81, 92245, Llunchi, UMMZ 84761; Loreto, USNM (JAP) 3742, USNM (GOV) 7292, 7324, 7410, Macuma, UIMNH 62868, USNM (JAP) 8650–52; Mera, KU 98626, 121324–26, 133533; Montalvo, USNM (GOV) 7287–88, 7408; Mount Tunguragna, FMNH 36623; Palmera, AMNH 36042; Paragachi, USNM (GOV) 7469; 8387; Plan de Milagro, USNM (JAP) 7024; Pucayacu, USNM (GOV) 7297; Puyo, AMNH 36043–44; Riobamba and Canelos, AMNH 35926, headwaters of Río Bobonaza, USNM (JAP) 8613; Río Corrientes, USNM (GOV) 7294; Río Cotopino, USNM (GOV) 7298; Río Curaray, FMNH 23486; region of upper Río Curaray, USNM (JAP) 3756; USNM (GOV) 7293, 7412; Río Napo, UMMZ 88966; Río Negro, KU 121327–28; Río Oglan, USNM (GOV) 7419; Río Pas-

taza, UMMZ 88967–68; upper Río Pastaza, USNM (JAP) 7938; north bank of Río Pastaza, between Baños and Abitagua, UMMZ 92022, 92029; Río Pindo, near Río Tigre, USNM (GOV) 7409, 7414–15; Río Pucuno, USNM (GOV) 6129; Río Sano, UMMZ 92028; Río Siquino, USNM (GOV) 7326, 7417–18; Río Villano, USNM (GOV) 7411; Río Suno, UMMZ 92031; Río Talin, USNM (GOV) 7295; San Francisco, UMMZ 88965; San José Viejo de Sumaco, USNM (GOV) 7276; Santa Cecilia, KU 105408, 105414, 109839, 112274, 148352–54, 152517, 158535; "Santiago/Zamora", UMMZ 82885; Shell Mera, USNM (GOV) 7284–85; Tiputini, USNM (JAP) 8626. PERU: no specific locality, ANSP 3702, 11294–95, 11539, 14282, 14284, 41289, 14301, FMNH 40045, MCZ 16356–57; Achinamisa, AMNH 52937; Ayendama, AMNH 52524, 52729; Balta, LSUMZ 14599–600, 28002–03; ridge between two Biabos, AMNH 52896; Cashiboya, AMNH 52915, 52866–68; Centro Unión, TCWC 42116–17; 44681, 44579, 44081–85, 40546–52, 40554; Cerros del Sira, AMNH 104292; Chanchamayo, AMNH 52188, 52691, FMNH 39642, 40639, 152302; Chancharía, USNM 193786; Chiaco-Bagua, MCZ 120277; Chipurana, AMNH 52209, 52218; Contamana, AMNH 52242; Estera Rohyana, AMNH 106268; Estirón, MZUSP 4378–79, 4384; Fundo Lotta, USNM 196057; Hacienda Pampayacu, MCZ 42404–05, 42418; Huacamayo, AMNH 21160; Igarapé Champuia, MZUSP 3344; Indiana, TCWC 44678; Iquitos, AMNH 52053, 52112, 52136, 52161–62, 52206, 52228, 52314, 52331, 52374, 52408, 52423, 52428, 52485, 52497, 52538–39, 52577, 52591, 52593, 52613, 52616, 52634, 52641, 52643, 52659–60, 52663, 52743–44, 52762, 52772, 52876–77, 52957, 52971, 52999, 53002, 53051, 53055, 53150, 53261, 53263, 53334, 53398, 53403, 53500, 54299, 54387, 54847, 54943, 55950, 56041, 56082, 56085, 56107–08, 56128, TCWC 38221, 39098, 40553, 41751, 44086–87, 44679, 46279, 47147–49, USNM 197272–78; Jenaro Herrera, MHNG 1567.81; Juliaca, AMNH 2959 (in error); La Divisioria, Sierra Azul, AMNH 107814, FMNH 56163–69; La Mar, Silva, FMNH 39642; Marcapata, FMNH 59175, 62956; Madre de Dios, FMNH 40039–41, 40234–35; Mishana, TCWC 42113–14, USNM 197272 (2); Monte Alegre, AMNH 52783; Monte Carmelo, AMNH 55548, 55555, 55622, 55627, 55629, 55634, 55636, 55641, 55645, 55653, 55655–56, 55918; Morona Cocha, AMNH 53135; Moropon, TCWC 38129–20, 38222, 42115, 44672–77, 39101; Moyobamba, BMNH 74.8.4.20, 74.8.4.69; FMNH 5715; Nazareth, FMNH 5673; Orellana (Reforma), AMNH 52095, 52909, 55670; Oxapampa, FMNH 134479; Pachisa, AMNH 52565; Pacaya, AMNH 53597; near Palca, FMNH 134470; Pampa Hermosa, Río Cushabatay, AMNH 53377, 53403, 53425–26, 53502, 53509–12, 53514–17, 53522, 55450, 55474, 55713, 55720–21, 55739, 55747, 55763, 55755–66, 55770, 55792, 55794, 55798, 55837, 55851, 55854,

55856, 55858, 55860–61, 55895, 55961, 55982, 55986, 55999, 56005, 56008–09, 56022; Pampa Hermosa, Río Ucayali, AMNH 52023–26, 52030, 53550, 53576–77; Panya, AMNH 52281, 52347–48; Paraíso, TCWC 42112; Parinari, AMNH 55680; Parvenio, AMNH 52457; Petras, ANSP 11469, 11671; Pozuzo, FMNH 5579; Puerto Mairo, FMNH 3678; Pucallpa, AMNH 71157-58; Punga, AMNH 52039, 52041, 52081, 52387, 53482–83, 56045, Quince Mil, FMNH 168384; 40 km NE Quince Mil, LSUMZ 32553; Quinton, AMNH 21161; headwaters, Río Aspusana, AMNH 52096; Río Itaya, near Iquitos, AMNH 52109, 52111, 52221, 52676, 52802, 53653, 53710, 53176, 53758, 53775, 53811, 53818, 54038, 54073, 54086, 54096, 54136, 54267, 54292, 54303, 54376, 54394–96, 54399, 54401, 54407, 54417, 54419, 54458, 54666, 54669, 54713, 54723, 54726, 54745, 54750, 54778, 54977, 55026, 55054, 55079, 55106–07, 55124, 55158, 55166, 55173, 55194, 56113, 56116; upper Río Marañon, BMNH 1913.6.4.5–6; upper Río Nieva, AMNH 55901; Río Putumayo, FMNH 37436; Río Samiria and Parinari Canyon, AMNH 5271, 57299–302; upper Río Ucayali, AMNH 71135, 7111–14; Río Ucayali, UMMZ 51254 (2); Roaboya, AMNH 52235, 52477, 52482, 52799, 52888, 53095, 54433, 55690–91; Sacanche, USNM 196056; San Ramón, FMNH 152302; Sarayacu, BMNH 81.5.13.37; Sobral, AMNH 55350, 55345; Suhuayo (Contamana) AMNH 53007; Suhuaya (Rean Rean), AMNH 53578; Tingo María, USNM (WS) 3113, USNM 193767–85; Tocache Nuevo, USNM 196058; Utuquina, AMNH 52938; Valle de Iscozazin, Chontilla, LACM 76806; Yanamono, TCWC 39099–100, 42118, 44080, 44680; Yarinacocha, FMNH 45591, 56123–24, 56145–49.

Liophis reginae zweifeli.—GUYANA: Mabaruma Compound, USNM 164207–10; north slopes of Mount Roraima, BMNH 1971.1724. TRINIDAD: no specific locality, BMNH 1947.3.3.27, USNM 17757–58; Arima, AMNH 81462; Arima-Blanchiceusse Rd., AMNH 73136; Brickfield, FMNH 49958; Mayaro, MCZ 49069; Mount Aripo, BMNH 1940.3.11.85; Rio Grande Forest, Sangre Grande, AMNH 81464, 85953; San Rafael, FMNH 49957; Tamana Caves, Mount Tamana, MCZ 100654; near Valencia, MCZ 81517; Vega de Dropouche Rd., AMNH 85954. VENEZUELA: Aricagua, BMNH 1905.5.31.55; Arabopó, UMMZ 85279; Caracas, MHNG 367.56, MBUCV 505; 9 km S Caracas, USNM 196332; Caripito, AMNH 67877–78, 98260–61; Carúpano, ANSP 5510; Capibara, USNM (FN) 35446; Cerro Turumiquire, AMNH 29317, FMNH 17833–36; Cerro Yapacana, RMNH 2276, 2285; Cuchiuano, AMNH 29332; Cumaná, UMMZ 56038; El Estánque, Borburata, MBUCV 3082; El Junquito, MBUCV 3083, SCN 4318; El Limón, CM 7355; El Vigía, CM 8001; El Yaque, Near Turumiquire, CM 7969; Los Canales, Naiguatá, CM 22780; 4 km NW

Montalbán, USNM (FN) 19641; 2.7 km NE Peña Blanca, KU 167586; planta eléctrica de Curpupao, AMNH 59430; Puerto Cabello, UIMNH 93850; Rancho Grande, AMNH 98262, BMNH 1970.237, CAS 138485, FMNH 204477, KU 167585, MBUCV 95–96, 621, 659, 3076–81, MCZ 62496, 81518, SCN 15103, UIMNH 22663, 63600, UMMZ 124225–33, 128390; San Antonio de Maturín, MCZ 9979; 5 km S San Juan de las Galdonas, RMNH 2363; Sorte, Chivacoa, SCN 10551; Viverios Guayabal, altos de Pipe, MCZ 112411.

Liophis reginae subsp.—TOBAGO: Pigeon Peak Trace, USNM 228069.

Liophis reginae semilineata × *L. r. macrostoma.*—ARGENTINA: Río Pescado, Oran, IML 115; Salta, IML 600. BOLIVIA: Chamblaya, BMNH 1902.5.29.96. BRAZIL: Porto Velho, Río Tapirapés, MZUSP 3751, 3752, 3797, 4326, 4336, 4362.

Liophis reginae reginae × *L. r. zweifeli*—GUYANA: Berbice, BMNH 53.4.6; Demerara, BMNH 55.8.28, 55.8.28.48; Dunoon, UMMZ 53912, 53968—69; Kartabo, AMNH 18170, 67876; Lama Creek, AMNH 36105; Matali, AMNH 61541; Stabu, FMNH 30959, 30962.

Liophis williamsi.—VENEZUELA: Cerro El Avila, UIMNH 63607: Colonia Tovar, CM 7393, USNM 121206; El Junquito, MCZ 51329; Rancho Grande, MBUCV 3044, UMMZ 124221, 124224.

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